Pl. Syst. Evol. 204: 39–48 (1997)

Plant Systematics and Evolution

Comparative embryology of three *Gentianaceae* species from the Central Caucasus and the European Alps

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Received November 27, 1995; in revised version April 11, 1996

Key words: *Gentianaceae, Gentiana pyrenaica, Gentianella caucasea, Gentianella germanica.* – Functional embryology, antipodals, endosperm, life history, seed development.

Abstract: A comparative investigation was carried out on the ovule and seed development of three mountain species of *Gentianaceae*, the perennial species *Gentiana pyrenaica*, and the two short-lived monocarpic species *Gentianella caucasea* and *G. germanica*. In all three species most embryological characters conform to those generally found in the family of the *Gentianaceae*. In some features, however, *G. pyrenaica* and the two *Gentianella* species differ from each other. In *G. pyrenaica* the ovule is anatropous, the integument 8–10 layered and the three reduced antipodals degenerate soon after fertilization. In contrast, *G. caucasea* and *G. germanica* form a hemitropous ovule, a 4–5 layered integument and up to 16 antipodal cells by secondary multiplication. All three species exhibit differences in synchronization between embryogenesis and endosperm development. Functional relations between the antipodal structure and the dynamics of seed development of the investigated species are postulated.

The genera *Gentiana* and *Gentianella* together comprise about 450 species, distributed mainly in mountain regions of Asia, Europe and America (Meusel & al. 1978). Most *Gentiana* species are perennials, whereas *Gentianella* species are annuals, biennials or short-lived perennials. Up to now, embryological investigations have been carried out on only about 30 species of these two genera (Shamrov 1987). In most cases they conform to the general embryological characteristics of *Gentianaceae*. Structural features vary in some details, however, providing valuable characters for classification.

In the present study, ovule and seed development of the perennial species *Gentiana pyrenaica* L., and the short-lived monocarpic species *Gentianella caucasea* (Loddiges ex Sims) Holub and *G. germanica* (Willd.) Börner are characterized and compared. To our knowledge *G. pyrenaica* and *G. caucasea* have not been investigated previously, and for *G. germanica* only the female gametophyte has been described (Guérin 1903). Both *Gentianella* species are rather similar in habit and morphological traits but occur as numerous ecotypic variants with different flowering times. Therefore investigating the extent to which these species share embryological characters seemed worthwhile. On the basis of the embryological profile of the three investigated species, possible connections between the structur-

al pecularities, the life histories, and the dynamics of seed formation are presented.

Material and methods

Plant material. *Gentiana pyrenaica* (syn. *Gentiana djimilensis* C. KOCH) is a perennial mountain plant distributed in the Pyrenees, the Carpathians, in SW Bulgaria, Anatolia and Iran, and in the Caucasus (GAGNIDZE 1985, TUTIN & al. 1972). In the Central Caucasus this species can be found between 2000 and 3500 m s.m. Depending on the altitude the flowering period is June to July, with a possible second flowering in August to October. The plant material for the present investigation was collected in July at 3100 m s.m. in the subnival zone on Mt. Sabertse in the Central Caucasus (Kazbegi region, Georgia).

Gentianella caucasea (syn. *Gentiana caucasica* BIEB.) is an annual plant, distributed in Anatolia, Iran and in the Caucasus (GAGNIDZE 1985). Various morphological types with different flowering times from summer to late autumn occur in widely differing habitats from the subalpine to the subnival zone (AKHALKATSI & WAGNER 1996). Plant material was collected in July at 1950 m s.m. in the subalpine zone on the lower slopes of Mt. Kuro in the Central Caucasus (Kazbegi region, Georgia).

Gentianella germanica (syn. *Gentiana germanica* WILLD.) is an annual or biennial species, occurring from the colline up to the alpine zone in West and Central Europe and in the mountain regions of the Balkans (MEUSEL & al. 1978). Like *G. caucasea*, this species occurs in ecotypic variants, showing differences in their morphological characteristics and time of flowering (WETTSTEIN 1895, ZOPFI 1991). The plant material was sampled in October from a biennial population at 2000 m s.m. in the subalpine zone of the Mt. Patscherkofel in the Central Alps (Tyrol, Austria). Herbarium vouchers of *G. pyrenaica* and *G. caucasea* are deposited in the herbarium of the Institute of Botany of the Academy of Sciences, Tbilisi (TBI). Voucher specimens of *G. germanica* are deposited in the herbarium of the University Institute of Botany, Innsbruck (IB).

Methods. Buds, flowers and fruits at different stages of development were fixed in FPA_{50} (formalin, propionic acid, 50% ethanol, 5 : 5 : 90) and stored in 70% ethanol. Ovules and seeds were dissected out of the ovaries, mounted on microscope slides in clearing solution according to HERR (1971) and examined with a microscope equipped with differential interference contrast optics. Mature seeds were cut into slices with a razor blade before mounting. Photographs were taken with an OLYMPUS Photomicrographic System, using KODAK Technical Pan 135 film at ISO 25 developed in AGFA Rodinal. For each of the species the lengths and widths of 50 seeds and the lengths of 20 embryos were measured at 100× magnification with an ocular micrometer.

Results

The gynoecia of the investigated species are superior, unilocular, bicarpellate (very rarely tricarpellate) and paracarpous; they are terminated by a short style and a 2-lobed stigma. In *Gentiana pyrenaica* the gynophore measures 7–8 mm, in *Gentianella caucasea* and *G. germanica* 3–4 mm and 3–5 mm, respectively. Numerous ovules develop on the parietal placentae along the fused margins of the carpels.

Gentiana pyrenaica. The ovule is anatropous, tenuinucellar and unitegmic (Fig. 2 A). The single integument consists of 8–10 layers of cells and forms a long micropyle. At the micropylar end the nucellus consists of only one cell layer, which degenerates during the extension of the embryo sac (Fig. 2 B). As is common in *Gentianaceae* (BOUMAN & SCHIER 1979, SHAMROV 1987), no vascular bun-